HOTSPOTS AND BEHAVIORAL PATTERNS OF SOUTHERN ALASKA RESIDENT KILLER WHALES (*ORCINUS ORCA*)

By

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Abstract

The resident killer whale (*Orcinus orca*) is a genetically and behaviorally distinct ecotype of killer whale that feeds primarily on Pacific salmon (*Oncorhynchus* spp.). Long-term monitoring over 30 years of study has enabled detailed investigation into pod-specific, seasonal, and compositional differences in space use and behavior. To investigate use of habitat, 33 resident killer whales representing 14 pods in the northern Gulf of Alaska were tagged with satellite transmitters during all years from 2006 to 2014, and transmissions were received during the months of June to January. Core use areas were identified through utilization distributions using a biased Brownian Bridge movement model. Tagging results indicate different core use areas between pods, which could be due to cultural transmission within matrilineal groups. To investigate differences in behavior, 1337 hours of behavioral data were collected from 2006 to 2015. For these observations, chi squared tests were used to determine significant differences in behavior budgets between seasons, regions, haplotypes, and numbers of pods. The presence of 'rarely sighted' pods (sighted in less than 5% of encounters) had a large influence on the frequency of social behavior, which increased from 18.5% without their presence to 31.4% with it ($X^2 = 17.3, df = 1, P < 0.001$). Frequency of social behavior was also significantly affected by the number of pods present ($X^2 = 72.8, df = 3, P < 0.001$), and increased from 4.7% to 31.2% with one pod to more than four pods present. Strong seasonal and pod-specific differences were found in core use areas, possibly driven by the availability of seasonal salmon migration. Social behavior, and to some extent foraging and resting behaviors, appear to be driven by group composition and numbers of pods throughout the spring to fall seasons. Overall, these findings help clarify spatial and behavioral patterns observed for resident killer whales.

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Acknowledgements: I cannot express enough gratitude to my parents for life-long encouragement and support. I would like to thank my committee for all of their realism, encouragement, and gentle prodding. Thanks to Dr. Josh London and David Douglas for guidance with statistical analysis of spatial data, Mayumi Arimitsu for review of the text, and Bryce Mecum for assistance with R coding and graphics. I would like to also thank John Durban, Graeme Ellis, Volker Deecke, Lance Barrett-Lennard, Harald Yurk, H?elena Symmonds, and Paul Spong for their insights and encouragement when I was first learning acoustic dialects in 2006.

Dedication: This thesis is dedicated to Eva Saulitis, who committed much of her life to studies of the AT1 transient killer whale population. While working as a tour-boat captain in 2004, I played a recording for Eva (via VHF radio) that I had just made of one lone killer whale in Thumb Cove, Resurrection Bay. Eva was returning with Craig Matkin from a research cruise in Prince William Sound, and was yet still several miles away. Upon hearing my recording, Eva immediately exclaimed - "That is one of the AT1's, trying to get in touch with the rest of its

pod!" Sure enough, Craig and Eva arrived later to photograph AT9, "Chenega", who soon met up with AT10, "Mike", and AT18 "Marie" (all members of the AT1s, as predicted). Prior to that day I had no idea that it was possible to identify killer whale groups by their calls. I was inspired to begin my journey in the study of acoustic dialects for Alaskan killer whale pods. This year we lost Eva to cancer. She held a strong belief that life didn't end, but rather passed on to those who came after, like leaves falling from a tree in autumn to give nutrients and new life to the forest. I can only hope that I carry on her passion to understand these amazing creatures, and share that passion with those around me.

General Introduction

The resident killer whale (*Orcinus* orca) is a genetically distinct piscivorous ecotype of killer whale found only in the North Pacific Ocean (Hoelzel et al., 1998; Morin et al., 2010; Parsons et al., 2013). They have diverged behaviorally, genetically, and acoustically from other sympatric ecotypes of killer whales, including the 'transient' killer whale ecotype, which eats mammals (Ford et al., 1998; Heimlich-Boran, 1988), and the 'offshore' killer whale ecotype which preys on sharks and other fishes (Ford, Ellis, et al., 2011). The 'resident' ecotype has been observed feeding exclusively on fish, primarily Pacific salmon (*Oncorhynchus spp.*), and has never been observed feeding on mammals or sharks (Ford et al., 1998; Ford et al., 2016; Saulitis et al., 2000). Scale and tissue samples collected during predation events indicate Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum salmon (*O. keta*) as primary prey for resident killer whales in the northern Gulf of Alaska (Matkin et al., 2013; Saulitis et al., 2000). The seasonal nature of salmon returns has been indicated as a driver for observed social activity in large multi-pod aggregations (Hoelzel 1993).

Resident killer whales typically spend their entire lives within their natal matrilines, which consist of a female, all of her adult offspring, and the offspring of females born to her (Bigg et al., 1990; Matkin et al., 1999). Dispersal from the natal matriline is rare in Washington, British Columbia and Alaska (Barrett-Lennard, 2000; Parsons et al., 2009). Killer whale pods are defined as social units consisting of related matrilines that are together during more than 50% of sightings and are believed to have common lineage (Bigg et al., 1990).

Killer whale pods and matrilines transmit cultural traditions through generations, including acoustic repertoires and call types (Filatova et al., 2015; Ford 1991; Yurk et al., 2002).

The relatedness of calls within these pods and matrilines parallel genetic relatedness (Yurk et al., 2002). Cultural transmission is also believed to contribute to similarities in travel patterns between groups (Similä et al., 1996), hunting and feeding techniques (Guinet & Bouvier, 1995; Similä & Ugarte, 1993), and beach rubbing (Rendell & Whitehead, 2001). Pod-specific use of habitat has been documented for the southern resident killer whale (SRKW) population (Hauser et al., 2007), but has yet to be reported in Alaskan waters.

Two primary genetic haplotypes (and a rare third one) are the only haplotypes known to occur amongst resident killer whales in the northern Pacific Ocean, from Washington State to Japan (Parsons et al., 2013). The southern resident (SR) haplotype was first described as the exclusive haplotype for the SRKW in Washington State/British Columbia, and the northern resident (NR) haplotype was first described as the exclusive haplotype of the northern resident killer whale population (NRKW) in British Columbia (Barrett-Lennard, 2000). From genetic studies of residents in Alaska, 65 sampled individuals share the NR haplotype with the NRKW population in British Columbia, and 54 sampled Alaska individuals share the SR haplotype with the SRKW population in Washington State and British Columbia (Craig Matkin, North Gulf Oceanic Society, unpubl. data). A third resident haplotype has only been documented once, in the Aleutian Islands (Parsons et al., 2013). Pods that share the same genetic haplotype are generally believed to share an ancestral maternal lineage; however, equivalent haplotypes may also occur through convergent evolution (Barrett-Lennard, 2000). Microsatellite genotypes suggest weak separation between NR-haplotype Alaska residents and NRKW, and stronger separation between the SR-haplotype Alaska residents and SRKW (Barrett-Lennard, 2000).

Mating among resident killer whales is more likely to occur between pods that are acoustically and genetically dissimilar (Barrett-Lennard, 2000; Ford, Hanson, et al., 2011; Yurk

et al., 2002). In Prince William Sound and Kenai Fjords, mating is known to occur between pods with different genetic haplotypes (Barrett-Lennard, 2000). The northern Gulf of Alaska is one of only a few regions where the NR and SR haplotypes are sympatric (Parsons et al., 2013). Thus, comparison of behavior by whales of different haplotypes is possible.

Resident killer whales travel in larger groups than transient killer whales, which could be due to differing foraging strategies (Baird & Dill, 1996). Typical resident pod size ranges from 3 to 50 individuals (Bigg et al., 1990; Ford et al., 2000; Morton 1990). Large group sizes may optimize efficiency while foraging on schooling fish; however, there is likely an upper group size limit at which foraging efficiency begins to be compromised (Ford et al., 1998). Multi-pod aggregations have been observed exceeding 100 individuals (Bigg 1987; current study). It has been suggested that these large groups occur for mating purposes, reinforcing social bonds between matrilines or pods, and as opportunities for juveniles to learn mating and reproductive skills (Filatova et al., 2009; Matkin et al., 1997). Vocal activity is typically very high in large aggregations (Ford 1989).

Satellite telemetry is a useful tool in describing core use areas, and is a method that is less subject to bias than boat surveys, which are limited by weather, survey locations, and daylight hours. Telemetry has also proven to be a useful tool in describing important areas for many cetacean species, such as false killer whales (*Pseudorca crassidens*), narwhals (*Monodon monoceros*), humpback whales (*Megaptera novaeangeliae*), and Hectors dolphins (*Cephalorhynchus hectori*) (Baird et al., 2013; Heide-Jørgensen et al., 2002; Kennedy et al., 2014; Rayment et al., 2009).

As an apex predator, resident killer whales are important to monitor for both conservation and management, particularly due to their strong preference for salmon. In the present study,

location data from satellite tags deployed on 33 individual animals in the northern Gulf of Alaska were used to assess core habitat use. Seasonal differences between core use areas were documented from June through October, and variation in core use between pods was described. Behavioral data was collected from 339 survey encounters to analyze changes in behavioral budgets. The hypothesis is that distinct differences occur in core habitat throughout the seasons, and that pod-specific use of the region is not random. A second hypothesis is that large multi-pod gatherings are purposeful, and that social and reproductive activities are tied to group composition.

Chapter 1: Shifting Hot Spots: Seasonal and pod-specific habitat use by resident killer whales in the northern Gulf of Alaska[1]

1.1 Abstract

The resident killer whale is a genetically and behaviorally distinct ecotype of killer whale (*Orcinus orca*) that feeds primarily on Pacific salmon (*Oncorhynchus* spp.). Details regarding core use areas have been inferred by boat surveys, but are subject to effort bias and weather limitations. To estimate a less-biased use of space, 33 resident killer whales representing 14 pods in the northern Gulf of Alaska were tagged with satellite transmitters from 2006 to 2014, and transmissions were received during the months of June to January. Core use areas were identified through utilization distributions using a biased Brownian Bridge movement model. Distinct differences between these core use areas were revealed that are highly specific to season and pod. In June, July, and August, the waters of Hinchinbrook Entrance and west of Kayak Island were primary areas used, mainly by the AB, AI, and AJ pods. These same pods shifted their focus to Montague Strait in August, September, and October. Port Gravina was a focal area for the AD16 and AK pods in June, July, and August, but this was not the case in later months. AK and AD16 pods were responsible for seven of eight documented movements into the deeper fjords of Prince William Sound, and these fjords were not a focus for other groups. These temporal shifts in habitat use may be a response to the seasonal returns of salmon, though details on specific migration routes and timing for these fishes are limited. We found strong seasonal

[1] Olsen, D.W., Matkin, C.O., Andrews, R. A., Atkinson, S. 2016. Shifting Hot Spots: Seasonal and pod-specific habitat use by resident killer whales (*Orcinus Orca*) in the northern Gulf of Alaska. Submitted to: Deep Sea Research II

and pod-specific differences between core use areas. Future research should investigate pod differences in diet composition and relationships between core area use and bathymetry.

1.2 Introduction

Resident killer whales are a genetically distinct piscivorous ecotype of killer whale found only in the North Pacific Ocean (Hoelzel et al., 1998; Morin et al., 2010; Parsons et al., 2013). They have diverged behaviorally, genetically, and acoustically from other sympatric ecotypes of killer whales in the same region, including the 'transient' killer whale ecotype, which feeds on mammals (Ford et al., 1998; Heimlich-Boran, 1988), and the 'offshore' killer whale ecotype which feeds on sharks and other fishes (Ford, Ellis, et al., 2011). The 'resident' ecotype has been observed feeding exclusively on fish, primarily Pacific salmon (*Oncorhynchus spp.*), and has never been observed feeding on mammals or shark (Ford et al., 1998; Ford et al., 2016; Saulitis et al., 2000). Scale and tissue samples collected during predation events imply Chinook, coho, and chum salmon as primary prey for resident killer whales in the northern Gulf of Alaska (Matkin et al., 2013; Saulitis et al., 2000).

Resident killer whales typically spend their entire lives within their natal matrilines, which consist of a female, all of her adult offspring, and any of the offspring of females born to her (Bigg et al., 1990; Matkin et al., 1999). Dispersal from the natal matriline is rare in Washington, British Columbia and Alaska (Barrett-Lennard, 2000; Parsons et al., 2009). Killer whale pods are defined as social units consisting of related matrilines that are together during more than 50% of sightings, and are believed to have common lineage (Bigg et al., 1990). The relatedness of calls within these pods and matrilines parallel genetic relatedness (Yurk et al., 2002).

Killer whale pods and matrilines transmit cultural traditions through generations, including acoustic repertoires and call types (Filatova et al., 2015; Ford 1991; Yurk et al., 2002). Cultural transmission is also believed to contribute to similarities in travel patterns between groups (Similä et al., 1996), hunting and feeding techniques (Similä & Ugarte, 1993), and beach rubbing (Rendell & Whitehead, 2001). Pod-specific use of habitat has been documented for SRKW (Hauser et al., 2007), but has yet to be reported in Alaskan waters.

Satellite telemetry is a useful tool in describing core use areas, and is a method that is less subject to bias than boat surveys, which are limited by weather, survey locations, and daylight hours. Telemetry has also proven to be a useful tool in describing important areas for many other cetacean species, such as false killer whales (*Pseudorca crassidens*), narwhals (*Monodon monoceros*), humpback whales (*Megaptera novaeangeliae*), and Hectors dolphins (*Cephalorhynchus hectori*) (Baird et al., 2013; Heide-Jørgensen et al., 2002; Kennedy et al., 2014; Rayment et al., 2009).

As an apex predator, resident killer whales are important to monitor for both conservation and management, particularly due to their strong preference for salmon. In the present study, location data from satellite tags deployed on 33 individual animals in the northern Gulf of Alaska are used to assess core habitat use. Seasonal differences between core use areas are documented from June through October, and variation in core use is described between pods. The hypotheses are that distinct differences occur in core habitat throughout the seasons, and that pod-specific use of the region is not random.

1.3 Materials and Methods

1.3.1 Study area and animal selection

The study area spanned the northern Gulf of Alaska from Southeast Alaska to the Alaska Peninsula (Figure 1.1). The bays and passes of Prince William Sound, the Kenai Coast, Kodiak Island, and Cook Inlet are glacially carved and therefore relatively deep (300-500m), and experience strong tidal currents (Halverson et al., 2013). The coastwise portion of this study area includes the continental shelf, which extends from 30-170 km offshore. The shelf ranges in depth from 100 to 300m in this region, and is subject to a general E to W flow of the Alaska Coastal Current (Royer, 1981). Strong downwelling conditions in winter promote inflow into Prince William Sound through Hinchinbrook Entrance and outflow through Montague Strait, but this pattern is less distinct in the summer months as offshore downwelling conditions relax (Halverson et al., 2013).

Satellite tags were deployed on 33 killer whales amongst 14 pods between 2006 and 2014 in Prince William Sound and Kenai Fjords (Table 1.1). Given the extremely rare dispersal from matrilines (Barrett-Lennard, 2000), the movement of one individual was taken to be representative of the movements of its entire matriline and representative of its pod. Tagging locations were opportunistic, performed during photo identification surveys in Prince William Sound and Kenai Fjords (Figure 1.1).

1.3.2 Tagging method

Whales were tagged with low-impact, minimally percutaneous external-electronics transmitter (LIMPET) satellite tags (Andrews et al., 2008). Tag designs were Wildlife Computers (Redmond, WA) SPOT 5 (AM-240, B, and C), SPLASH10 (AM-266A and AM-

292A). Tags were deployed by crossbow or air rifle at a distance of 6-20 m from a 12 m survey vessel. Two 6.5 cm long titanium darts equipped with backward-facing barbs were used to anchor the tags in the connective tissue of the dorsal fin (Andrews et al., 2008). These transmitters sent ultra-high frequency (UHF) radio signals to Argos receivers onboard weather satellites. To conserve power, transmissions were limited to whale surface time by a submersion sensor.

1.3.3 Data Analysis

Locations were calculated by the Argos system using the method of least squares, and each location was assigned a location class. Location classes 3, 2, and 1 are assigned an accuracy estimate by Argos, with the 68th percentile error ranging from 0.25 to 1.5 km, while the remaining LCs (0, A, B, and Z) are not assigned an error. All location data were subsequently processed with the Douglas Argos Filter, based on location class and realistic movement parameters, including turning angles and distance ratios between positions (Douglas et al., 2012). For core use and home range analyses, the first 24 hours of data were removed from each deployment to minimize potential tagging site bias. Twenty four hours was considered sufficient because killer whales can make mean daily movements of over 100 km (Matthews et al., 2011; Williams & Noren, 2009).

Locations of core use areas were estimated using kernel density estimation and measured with utilization distributions (UDs). UDs are defined as the minimum area encompassing a certain probability of relocation (Kie et al., 2010; Seaman & Powell, 1996). Core use areas are defined as the 50% UD probability contour, and home range is defined as the 95% UD probability contour (Fieberg & Kochanny, 2013; Kie et al., 2010; Schuler et al., 2014). One

challenge with telemetry data and kernel density estimators is the potential for results to be biased by temporal and spatial autocorrelation. To minimize autocorrelation, UDs were estimated using biased Brownian Bridge models similar to the approach used for habitat use modeling of Pacific Walrus (*Odobenus rosmarus divergens*) in Alaska (Jay et al., 2012).

Utilization distributions were calculated for each pod, each month and year using the R package *adehabitatHR* (Calenge, 2011). A user-defined grid of 1,000,000 pixels was established over the entire area of received locations in order to assign the UD densities. However, cell size is reported to have little effect on the density distribution (Calenge, 2011). To adjust for variation in sample size due to tag transmission duration, UDs were first calculated for each animal, and the subsequent density values were weighted by the number of days of tag deployment. After summing the individual weighted densities, values were standardized so that the probability across the grid still summed to a value of 1.

To assess variability in habitat use, core use and home range areas were visually examined by pod, month, and year. Core use areas (50%) and home range areas (95%) were calculated using the kernel.area function. Probability polygons were created for 95, 80, 65, 50, 35, and 20%. These UDs were imported into QGIS for visual analysis and comparison of UD sizes by month, year, and pod. To examine temporal variation, seasonal and interannual variability were examined within the AJ pod, which had a large number of observations (241 days), and within the pooled AD16 and AK pods (152 days total), which are known to be closely related (Barrett-Lennard, 2000; Matkin et al., 1999). Home range (95%) sizes were calculated for each individual. The land portions of UD polygons were removed for home range and core use area calculations.

In order to limit erroneous calculations of short-term movements, speed and distance calculations were used only for positions that were separated by more than one hour and less than six hours. Speed calculations from Argos positions that are less than one hour apart can be greatly exaggerated by erroneous positions, and positions that are more than six hours apart could miss non-linear movements.

1.4 Results

Transmissions were received from 33 individual whales for a total of 965 transmission days between 2006 and 2014. During any given year, transmissions were received between the months of June and December, and also from one tag in January 2011 (Table 1.1). However, 91.9% of transmissions were received between June and October. The mean number of days that each tag transmitted was 26.1 days. Of the locations that passed the Douglas Argos Filter, none were received from beyond the continental shelf break (Figure 1.1). Median short-term movements were estimated at 4.43 km/hr, which extrapolates to 106 km/day.

Strong temporal shifts in core use areas were evident, particularly between summer and fall months. Hinchinbrook Entrance was a strong focal area for the AJ pod during June, July, and August, but was used much less in September and October (Figure 1.2). Montague Strait was heavily used in August, September, and October, but not in earlier months (Figure 1.2, 1.3). The waters west of Kayak Island saw consistent use in June, July, and August, but less use in September and October (Figure 1.2). Port Gravina was a focal area for the AD16 and AK pods during June, July, and August, but had no evident use during September or October (Figure 1.3).

Strong differences in core use were also evident between individual pods. The AB, AI, and AJ pods accounted for most of the use in Hinchinbrook Entrance and most of the use in

Montague Strait, and they were the only pods that demonstrated regular use of waters west of Kayak Island (Figure 1.4). The waters west of Kayak Island are likely important, as 12 out of the 16 tagged animals from the AB, AI, and AJ pods made at least one visit to the waters west of Kayak Island. The AB, AI, and AJ pods were also the primary pods to use offshore areas ranging as far as the shelf break. The AD16 and AK pods did not use offshore waters, and were the primary users of the northern edges of Prince William Sound, including the long glacially carved fjords (Figure 1.3). These two pods were responsible for seven out of the eight trips recorded into these long fjords. The AE pod used the inside waters of Prince William Sound, but was not observed using long fjords or offshore waters. The AD5 and AY pods were the primary pods to use Resurrection Bay and the waters adjacent to Shuyak and Marmot Islands, near the northern end of Kodiak Island (Figure 1.5).

A high percentage of positions in Montague Strait were located within a glacially carved trench that is 200-300 m deep (Figure 1.6). Within Montague Strait, 1346 of 2035 locations (66%) were in waters between 200 to 300 m in depth, even though this only represents 21% of the waters of Montague Strait. The 200-m isobath creates a clear boundary for the majority of these locations. This dynamic was not observed in other areas of Prince William Sound or the northern Gulf of Alaska.

The largest home ranges, by far, belonged to the tagged whales AF46, AG3, and AX110, at 26,874, 29,863, and 27,976 km^2 over 26, 21, and 50 days of tag deployment (Figure 1.7). However, whale AJ15 utilized a home range of only 17,727 km^2 over 102 days of deployment, and eight other tagged whales never exceeded home range sizes of 20,000 km^2 over tag durations of 42 to 76 days. The smallest home range for any tagged whale that exceeded 12 deployment days was 4,560 km^2, belonging to AE18 over 31 days. The home range for AE6 was similar,

with an area of only 5900 km^2 over 36 days. The median and mean home ranges in this study were 8925 and 10,309 km^2.

1.5 Discussion

Resident killer whales showed seasonal differences between core use areas in the northern Gulf of Alaska. Core use areas were specific to individual pods. The observed seasonal variation in core use areas may be related to the specific timing of returns of coho and chum salmon to their natal spawning streams, and the congregation of Chinook salmon while foraging in nearshore waters. Salmon make highly predictable seasonal returns to their natal streams, and Chinook, coho, and chum have been shown to comprise a major portion of the summer diet for resident killer whales in south central Alaska (Matkin et al., 2013; Saulitis et al., 2000). The arrival of resident killer whales and salmon has been shown to occur concurrently in British Columbia (Hanson et al., 2010), and Chinook and coho salmon have been shown to dominate the summer diet of resident killer whales in that area (Ford & Ellis, 2006; Ford et al., 2016). Survival rates for resident killer whales in British Columbia have been linked with abundance of Chinook salmon (Ford et al., 2010). In Alaska, prey samples have been collected at three of the high-use areas noted in this study, and these samples were dominated by scales from Chinook, coho, and chum salmon (Matkin et al,. 2013; Saulitis et al., 2000). Seasonal dietary shifts from Chinook to coho salmon have been documented in both Alaska and the Pacific Northwest (Ford et al., 2016; Matkin et al., 2013).

The Alaska Department of Fish and Game reports peak chum return timing to occur in late June in Prince William Sound (ADFG, 2002), which could be partially responsible for the high use of Hinchinbrook Entrance in early summer. Chum salmon scales from predation events

by resident killer whales have been collected in Hinchinbrook entrance in June (Matkin et al., 2013). Hinchinbrook Entrance is one of the two main entrances to Prince William Sound and is the primary influx for ocean waters to enter the sound (Halverson et al., 2013).

The high use in Montague Strait in late summer and fall coincides with large congregations of adult Pacific herring (*Clupea pallasi*) and humpback whales (*Megaptera novaeangliae*) that prey on them (Moran et al., 2015). Although herring are important in the diet of killer whales in Norway and Iceland, the technique for hunting them is evident from the surface (Samarra & Foote, 2015; Similä et al., 1996). Herring predation is very rare for well studied killer whales in the North Pacific based on observations from surface kill remains and scat analysis (Ford & Ellis, 2006; Ford et al., 2016; Saulitis et al., 2000). However, it is possible that this aggregation of herring attracts feeding Chinook and coho salmon.

Pod-specific habitat preferences described in the present study may be related to cultural transmission of learning through generations, as individuals swim with their mother or close relatives throughout their lives (Bigg et al., 1990). Cultural transmission has been documented amongst killer whale acoustic repertoires, foraging strategies, and habitat preferences (Guinet & Bouvier, 1995; Hauser et al., 2007; Similä & Ugarte, 1993; Yurk et al., 2002). Similar pod-specific core use patterns were noted in the San Juan Islands for SRKW (Hauser et al., 2007). Another possible cause of these patterns could be competition, but competition has not observed between unrelated pods. To the contrary, killer whale pods are often attracted to one another for social and reproductive reasons. They have been shown to mate outside of their natal pod, particularly with pods that are least genetically similar (Barrett-Lennard, 2000). Furthermore, closely related pods in this study demonstrated similar patterns of habitat use. The AB, AI, and AJ pods share the NR haplotype, and are the only pods shown to use offshore waters west of

Kayak Island and Hinchinbrook Entrance. AD16 and AK pods share the SR haplotype, and are the only pods to use upper fjords and focus on nearshore habitat. The very large linear range difference between the unrelated AE pod (roughly 200 linear km), which has the SR haplotype, and the AF and AG pods (1300 linear km), which have the NR haplotype, is striking. While this difference could be attributed to diet differences, it is more likely that these differences in linear range stem from social and reproductive behavior (Matkin et al.,1997).

Bathymetry appears to be important in some core use areas, and should be explored further. Our results show that the deeper waters (200-300m) of Montague Strait are important during summer and fall. Bathymetric features have been found to be preferential habitat for other delphinids (Dahood, 2009; Ingram & Rogan, 2002). Depth sensors were present on a limited number of tags in this study, and suggest that resident killer whales in this area regularly dive to or near the seafloor in 200-300m (Matkin et al., 2013). Chum salmon in Japan have been observed to dive to the bottom in response to presence of Dall's porpoise (*Phocoenoides dalli*) (Yano et al., 1984), and Chinook salmon have been documented diving 300-400m after release (Candy & Quinn, 1999). Furthermore, DTAGs deployed on NRKW in British Columbia documented the capture of Chinook, chum, and coho salmon as deep as 264, 164, and 165m respectively (Wright, 2014). If salmon aggregate in these deep basins near the entrances to avoid predation, or to feed on congregating forage fish such as herring, the use of deeper waters within Montague Strait and near Kayak Island could be explained. Interestingly, many other deep glacial trenches in the continental shelf do not appear to be important for these Gulf of Alaska resident killer whales during the summer and fall.

Alternatively, the deep waters of Montague Strait, Hinchinbrook Entrance, and Kayak Island could provide important foraging opportunities on benthic species, including Pacific

halibut (*Hippoglossus stenolepis*), lingcod (*Ophiodon elongatus*), and sablefish (*Anaplopoma fimbria*). It would be unlikely to collect tissue samples from predation events on these species at the surface if they were consumed in deeper waters. However, in spite of the availability of these potential prey species in other deep waters at the edge of the continental shelf and in the deep glacial trenches that cut across the shelf, these locations were not used much by tagged individuals in this study. Additionally, recent studies of killer whale fecal samples from SRKW in the San Juan Islands demonstrate similar findings to the surface collections of fish scale and tissue after predation events, which is that salmonid prey dominate the diet in summer months (Ford et al., 2016). The seasonality of use by killer whales in Montague Strait, Hinchinbrook Entrance, and Kayak Island also supports surface observations of salmon predation (Matkin et al., 2013; Saulitis et al., 2000).

One of the important revelations of this project, and one of the main advantages of satellite telemetry over other methods of habitat assessment, was the discovery of previously unknown core use areas. The region just west of Kayak Island appears to be important habitat, particularly in June, July, and August (Figure 1.2). Additionally, the areas SE of Marmot Island and NE of Shuyak Island appear to be important for at least the AD5 and AY pods (Figure 1.5). Due to the remote location and difficult weather conditions, these areas would not likely be revealed by boat surveys, which can be biased by survey effort (Baird et al., 2013). Interestingly, most of the use near Kayak Island was from AB, AI, and AJ pods, and nearly every tagged member of AB, AI, and AJ pods visited this area. In the future, passive acoustics may help detail the importance of these areas.

The variability described in this study serves as a caution for estimation of home range. Culturally influenced, pod-specific behavior appeared to have great impact on home range size

estimates. Home range sizes for individuals from AB, AE, AI, and AJ pods were all limited to 20,000 sq. km. or less, while individuals from AF, AG, and AX pods had home ranges of nearly 30,000 sq. km. These differences did not appear to be a result of tag transmission duration, and the home ranges based on these telemetry data are very similar to the geographic extent of photographic documentation. AB, AE, AI, and AJ pods have never been photographed beyond the relatively small range represented by the tag data, and the home ranges of AF and AG pods are also very similar to the photographic documentation, which extends from Kodiak to Southeastern Alaska (Matkin et al., 1997). Without consideration of these cultural and behavioral differences, any study that has a limited number of tags may only illustrate a subset of the population that is not representative of the whole.

The median short-term movement estimates of 4.43 km/hr (106 km/day) are similar to published movement rates for NRKW of 1.6 m/s (138 km/day) calculated by theodolite (Williams & Noren, 2009). This is likely a conservative estimate, as some non-linear movements are not always documented if there are gaps in the tag data.

The strong temporal patterns and pod-specific core use described in the present study should be considered in conservation management strategies. As an example, vessel traffic in the oil tanker lanes through Hinchinbrook Entrance may have a much larger impact on resident killer whales in June and July than in September and October, and impact by winter vessel traffic is largely unknown. Additionally, the AB pod, which lost 25% of it members after swimming through the Exxon Valdez Oil Spill in 1989 (Matkin et al., 2008), appears to depend heavily on Hinchinbrook Entrance, Montague Strait, and the waters west of Kayak Island. Restoration plans for this pod should consider the protection of these areas. Future research should

investigate the relationship between seasonal differences in core use and salmon migration routes, and also investigate wintertime use.

From this study there are two main conclusions. First, core use areas and home ranges in this population are highly variable between pods, which may be due to cultural transmission within matrilineal groups. Second, there are distinct seasonal changes in core use areas. These seasonal changes are most likely in response to the migratory return and feeding congregations of various species of salmon. Continued diet studies are warranted to investigate relationships between core use areas and the subsequent prey.

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1.8 Figures

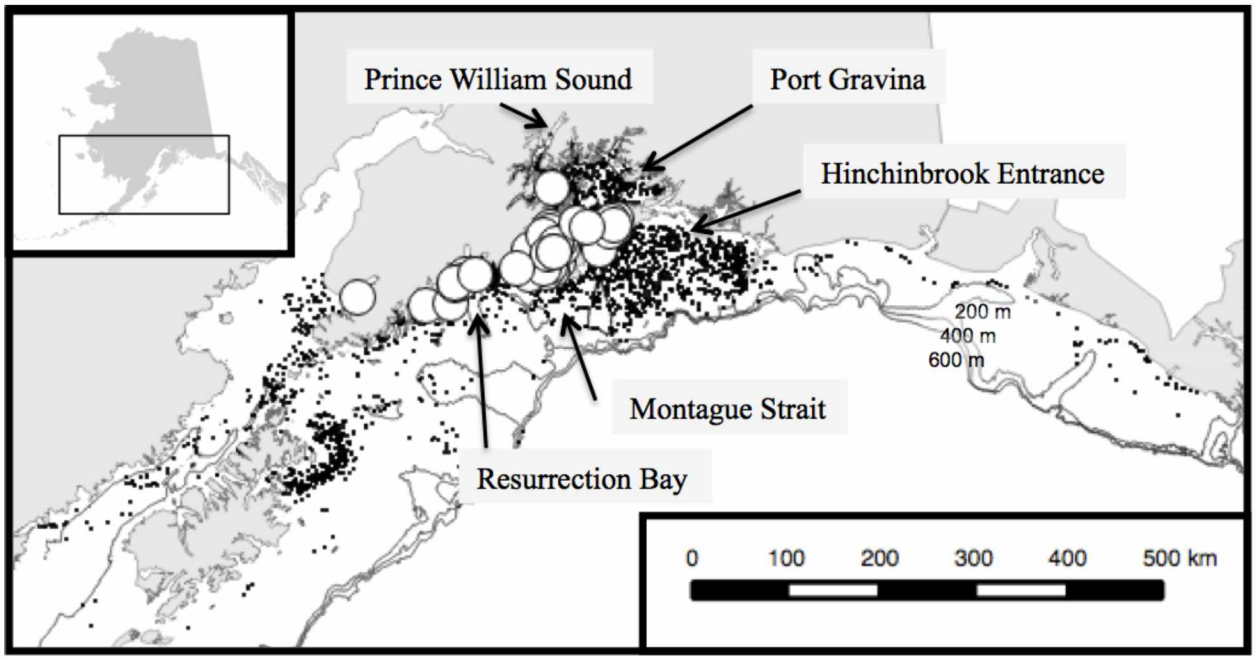

Figure 1.1 Study area for resident killer whales (*Orcinus orca*) with tag deployment locations (white circles), telemetry locations (black dots), and 200m, 400m, and 600m bathymetry contours.

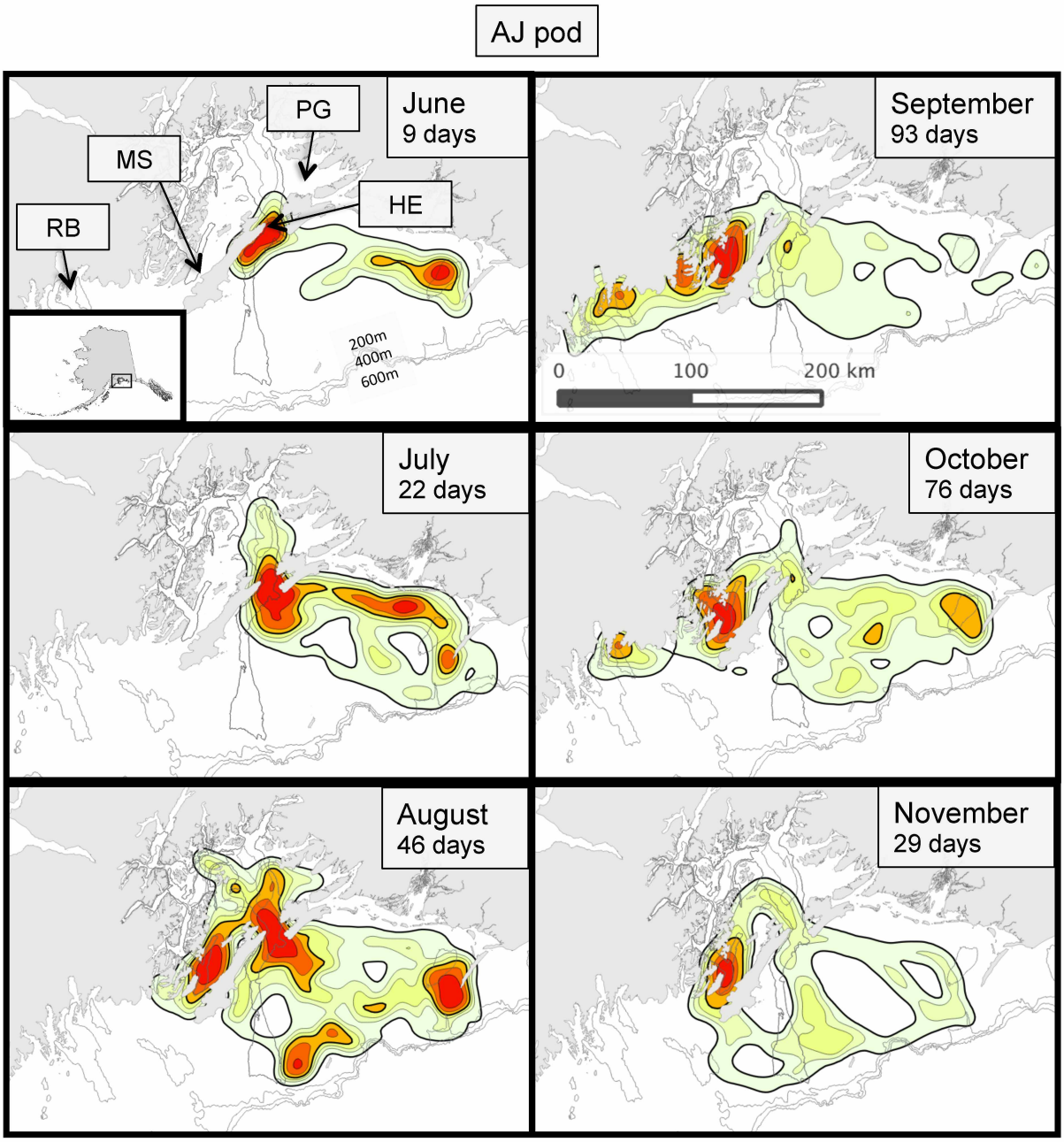

Figure 1.2 Monthly variation in space use by AJ pod of resident killer whales (*Orcinus orca*). Contour intervals are at 20, 35, 50, 65, 80, and 95% probability utilization distributions, 50 and 95% are also defined by bold lines. Locations are abbreviated as follows; RB=Resurrection Bay, MS=Montague Strait, HE=Hinchinbrook Entrance, PG=Port Gravina.

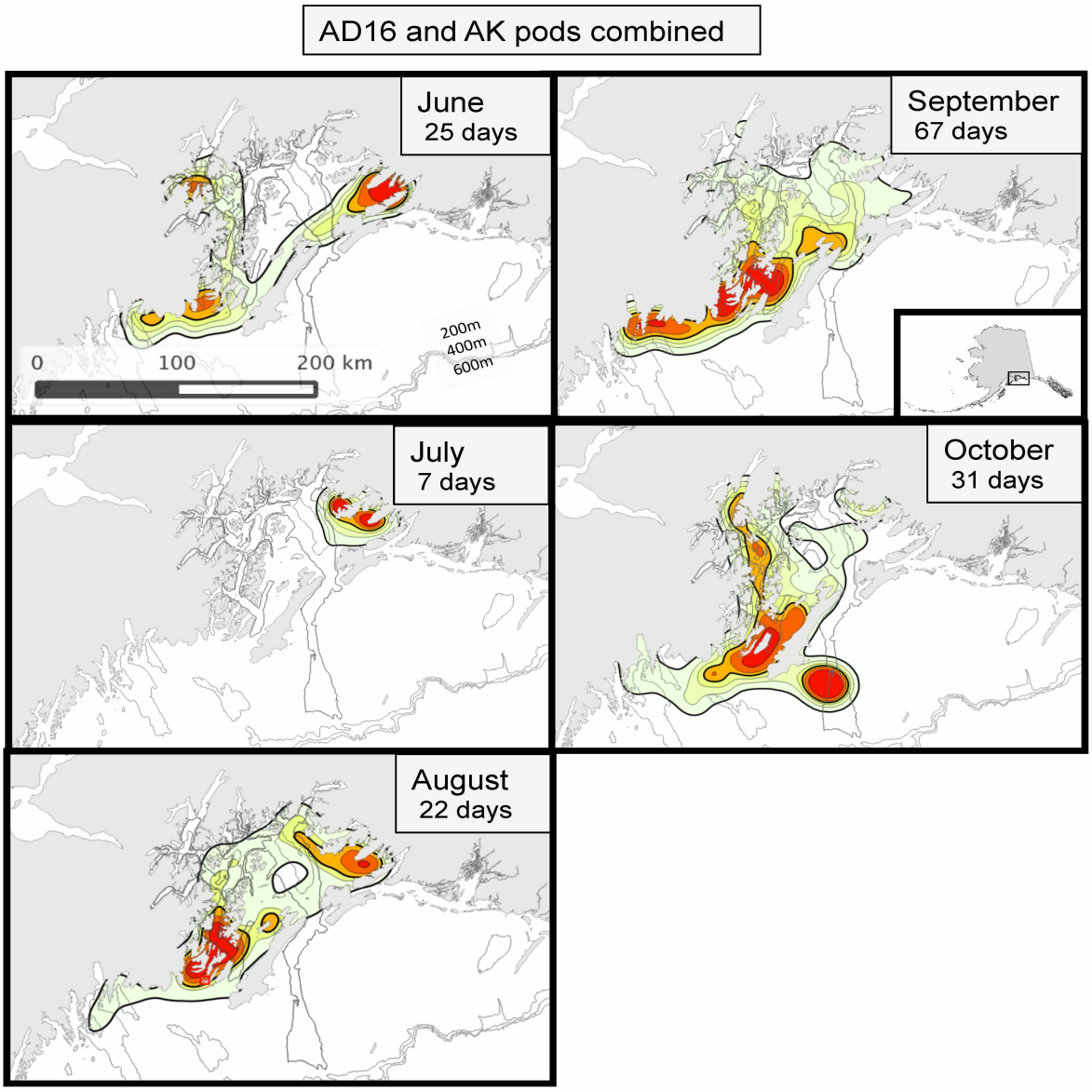

Figure 1.3. Monthly variation in space use by combined AD16 and AK pods of resident killer whales (*Orcinus orca*). Contour intervals are at 20, 35, 50, 65, 80, and 95% probability utilization distributions, 50 and 95% are also defined by bold lines.

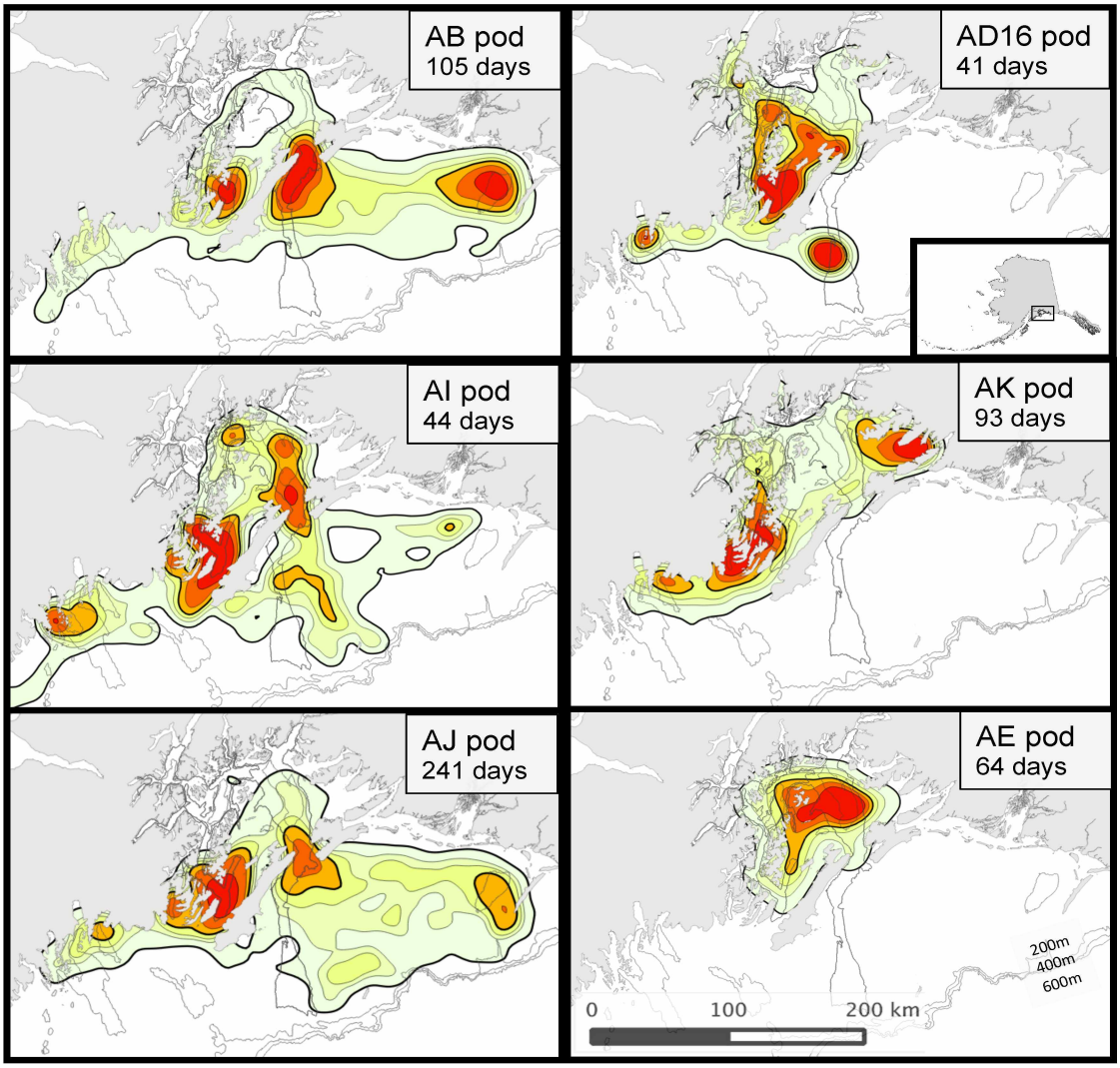

Figure 1.4. Pod-specific variation in space use for resident killer whales (*Orcinus orca*). Contour intervals are at 20, 35, 50, 65, 80, and 95% probability utilization distributions, 50 and 95% are also defined by bold lines.

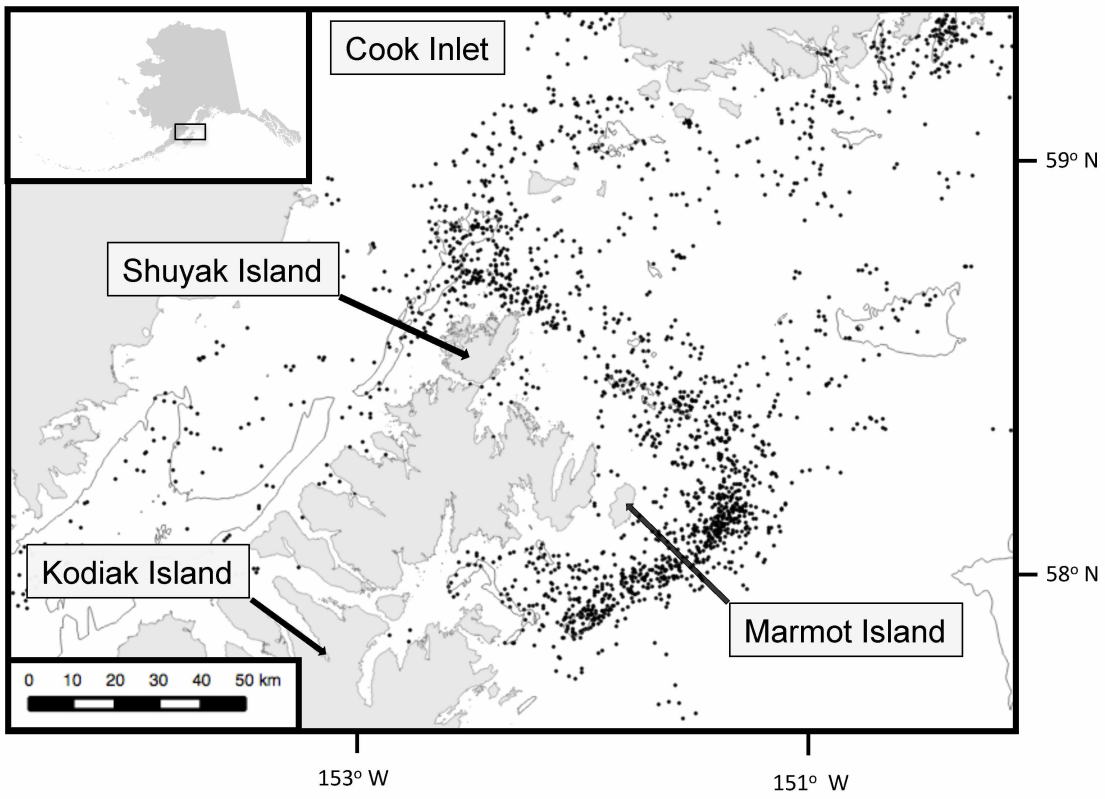

Figure 1.5. Potential areas of high use by killer whales (*Orcinus orca*) near Shuyak and Marmot Islands, telemetry locations represented with black dots.

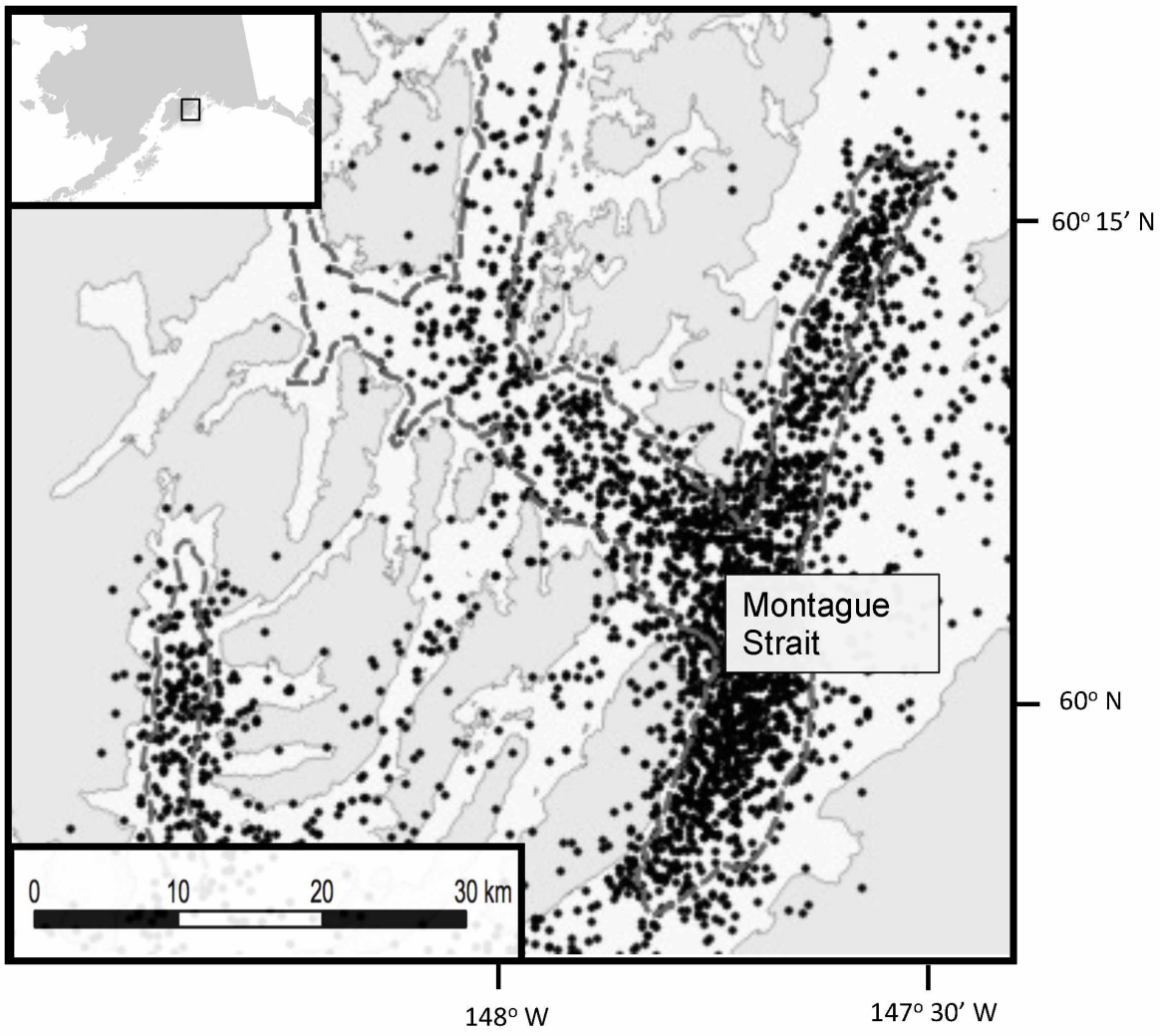

Figure 1.6. Lower Montague Strait with 200m bathymetric contour (dashed line) and telemetry locations.

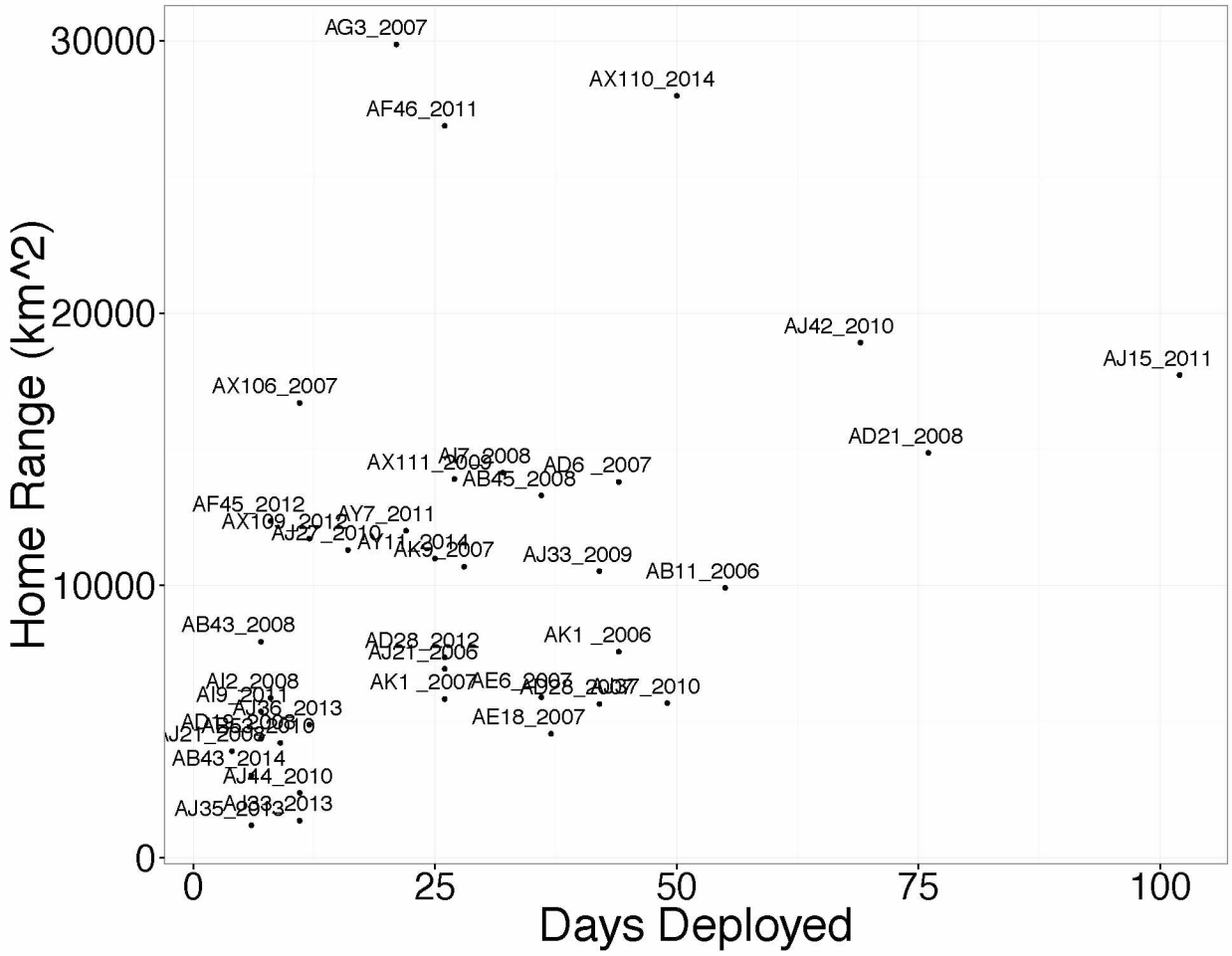

Figure 1.7. Killer whale (*Orcinus orca*) home range estimates (95% UD, km^2) by tag transmission duration.

1.9 Tables

Table 1.1. Number of transmission days from tagged resident killer whales (*Orcinus orca)*, by month and year 2006-2014.

	2006	2007	2008	2009	2010	2011	2012	2013	2014	Total
June	0	37	17	27	19	22	0	0	23	145
July	0	32	26	0	20	9	0	0	35	122
August	22	59	15	9	47	17	20	0	16	205
September	64	20	0	39	34	13	31	17	6	224
October	31	42	45	26	0	31	4	12	0	191
November	4	1	33	0	0	21	0	0	0	59
December	0	0	13	0	0	5	0	0	0	18
January	0	0	0	0	0	0	1	0	0	1
Total days	121	191	149	101	120	118	56	29	80	965

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Chapter 2: Behavioral Changes During Multi-Pod Aggregations of Southern Alaska Resident Killer Whales (*Orcinus orca*)[1]

2.1 Abstract

Between 2006 and 2015, 1352 hours of behavioral data were collected during 338 encounters with resident killer whale pods in Prince William Sound and the Kenai Fjords, Alaska, to assess seasonal, regional, group composition, and haplotype-specific differences in behavioral budgets. Frequency of four primary behaviors was compared; foraging, resting, socializing, and travelling. Chi squared tests were used to determine significant differences in behavior budget between seasons, regions, haplotypes, and numbers of pods. The presence of 'rarely sighted' pods (sighted in less than 5% of encounters) had the largest influence on the frequency of social behavior, which increased from 18.5% without their presence to 31.4% with it ($X^2 = 17.3, df = 1, P < 0.001$). Frequency of resting behavior decreased significantly with the presence of these 'rarely sighted' pods, 30.9% to 23.2% ($X^2 = 3.97, df = 1, P = 0.046$). Behavior was also significantly affected by the number of pods present ($X^2 = 78.9, df = 9, P < 0.001$). Frequency of social behavior was least for single pod encounters (4.7%), and increased with two pods present (16.1%), three pods present (21.2%), and four or more pods present (31.2%) ($X^2 = 72.8, df = 3, P < 0.001$). Frequency of foraging behavior decreased with the number of pods present, from 47.2% for single pod encounters to 31.9% with four or more pods present ($X^2 = 12.7, df = 3, P = 0.005$). No difference was detected in the behavioral budget between groups of different genetic haplotype, or by the presence of one versus two genetic

[1] Olsen, D.W., Matkin, C.O., Mueter, F.J., Atkinson, S. 2017. Behavioral changes during multi-pod aggregations of southern Alaska resident killer whales (*Orcinus orca*). Prepared for submission to: Aquatic Mammals.

haplotypes. Social behavior, and to some extent foraging and resting behaviors, do appear to be driven by the composition of the group encountered.

2.2 Introduction

The resident killer whale (*Orcinus orca*) is a piscivorous ecotype found only in the northern Pacific Ocean, and is genetically distinct from transient and offshore, two other sympatric killer whale ecotypes (Morin et al., 2010; Parsons et al., 2013). Residents feed primarily on Pacific salmon, travel consistently in matrineal groups, and make consistent pod-specific stereotyped calls (Bigg et al., 1990; Deecke et al., 2000; Ford & Ellis, 2006; Saulitis et al., 2000; Yurk et al., 2002). Regular seasonal movements and patterns of habitat use have been documented for the resident ecotype (Hauser et al., 2007; Matkin et al., 1997; Olsen et al., in review; Scheel et al., 2001), making the study of behavioral budgets a possibility.

Long-term photographic studies have consistently demonstrated that both male and female resident killer whales remain with their mother for the entirety of their lives (Bigg et al, 1990). Outmigration from these matrilineal groups is extremely rare (Bigg et al., 1990; Matkin et al., 1999). Pods are defined as groups of matrilines which are sighted together in more than 50% of photographic encounters (Bigg et al., 1990). These traits facilitate the assessment of behavioral budgets within the context of social groupings.

Resident killer whales travel in larger groups than transient killer whales, which could be a result of foraging strategies (Baird & Dill, 1996). Typical resident pod size ranges from 3-50 individuals (Bigg et al., 1990; Ford et al., 2000; Morton 1990). Large group sizes may optimize efficiency while foraging on schooling fish, however there is likely an upper group size limit at which foraging efficiency begins to be compromised (Ford et al., 1998). Multi-pod aggregations

have been observed exceeding 100 individuals (Bigg 1987; current study). It has been suggested that these large groups occur for mating purposes, reinforcing social bonds between matrilines or pods, and as opportunities for juveniles to learn mating and reproductive skills (Filatova et al., 2009; Matkin et al., 1997). Vocal activity is typically very high in large aggregations (Ford 1989). In Kamchatka is has been reported that resident killer whales alter their behavior in large multi-pod aggregations (Filatova et al., 2009).

Two primary genetic haplotypes (and a rare third one) are the only haplotypes known to occur amongst resident killer whales in the northern Pacific Ocean, from Washington State to Japan (Parsons et al., 2013). The SR haplotype was first described as the exclusive haplotype for SRKW in Washington State/British Columbia, and the NR haplotype was described first as the exclusive haplotype of the NRKW whale population in British Columbia (Barrett-Lennard, 2000). From genetic studies of residents in southern Alaska, 65 sampled individuals share the NR haplotype with the NRKW population, and 54 sampled individuals share the SR haplotype with the SRKW population (Matkin, unpubl. data). A third resident haplotype has only been documented in the Aleutian Islands, not in the current study area (Parsons et al., 2013). Pods that share the same genetic haplotype are generally believed to share an ancestral maternal lineage, however equivalent haplotypes could potentially occur due to convergent evolution (Barrett-Lennard, 2000). Microsatellite genotypes suggest weak separation between NR haplotype Alaska residents and the NRKW population, and stronger separation between the SR haplotype Alaska residents and the SRKW population (Barrett-Lennard, 2000).

Mating amongst resident killer whales is more likely to occur between pods that are acoustically and genetically dissimilar (Barrett-Lennard, 2000; Ford, Hanson, et al., 2011; Yurk et al., 2002). In Prince William Sound and Kenai Fjords, mating is known to occur between

pods with different genetic haplotypes (Barrett-Lennard, 2000). The northern Gulf of Alaska is one of only a few regions where the NR and SR haplotypes are sympatric (Parsons et al., 2013). Thus, comparisons of behavior by different haplotypes or combinations of them are possible.

Pod-specific ranges and long-distance movements have been documented for southern Alaska residents through long-term photographic monitoring and satellite telemetry, at times with pods far from the center of their known range (Matkin et al., 1997, Chapter 1). It has been suggested that these long-distance movements are undertaken primarily for social reasons (Matkin et al., 1997). In Prince William Sound and Kenai Fjords, these movements may result in large aggregations of resident killer whales, which include 'frequently sighted' and 'rarely sighted' pods. In this study, we test the hypothesis that southern Alaska resident social behavior during large aggregations is influenced by factors of group composition.

2.3 Methods

From 2003 to 2015, photo-identification based killer whale surveys were conducted in Prince William Sound and Kenai Fjords, in southern Alaska (Figure 2.1). This region is characterized by long glacially carved fjords, some of which open to the Pacific Ocean, and includes a large sound with complex passageways and entrances. Studies were conducted in the months of May through October from a 36' research vessel as a part of a long-term photographic monitoring program. Individuals that were photographed together more than 90% of the time were assumed to be members of the same matriline, and matrilines that were photographed together more than 50% of the time were assumed to be members of the same pod (Bigg et al., 1990). Each individual was assigned an alphanumeric label for identification (ID), e.g., AK007. With this assignment, the first letter represents Alaska, the second letter represents the pod, and

the numeral represents the individual. In the case where a pod was observed to travel together less than 50% of their time after being named with the same letter, the pod ID was designated by the ID of a prominent matriarch. For example, AD16 and AX48 pods are named after their matriarchs, AD16 and AX48.

We used behavioral category definitions that were originally defined by Ford (1989), and modified by Morton (1990), Felleman et al. (1991), and Barrett-Lennard et al. (1996). They were also used to describe behavioral differences between transient and resident killer whales in this study area, and to describe behavior and acoustics for the AT1 transient pod in Prince William Sound, Alaska (Saulitis, et al., 2000, Saulitis, et al. 2005). Milling and beach rubbing, which accounted for less than 1% of all observations, were not included in the analysis. The four included behaviors were defined as follows:

Socializing: Engaged in behaviors such as chasing, rolling, and aerial displays not related to feeding. Aerial displays included breaching, spy-hopping, and fluke- and flipper-slapping. Sexual behavior, indicated by erect penises, was also considered socializing. During socializing, vocal activity was high (Ford 1989).

Foraging: Engaged in search for, pursuit, capture, and consumption of prey. Foraging upon fish was indicated by echolocation (Barrett-Lennard et al., 1996) and sporadic tight circling and lunging by individual whales (Ford 1989; Hoelzel 1993). While foraging, the whales were widely dispersed, either singly or in small groups (Barrett-Lennard, et al., 1996).

Traveling: Swimming in a line-abreast pattern in one or more groups, moving in a consistent direction at speeds of over 6 km/h (Barrett-Lennard et al., 1996). Individuals typically swam within a few body lengths of their neighbors.

Resting: Movement and breathing patterns closely synchronized and moving at speeds much slower than those of traveling whales (<4 km/hr) (Ford 1989, Barrett-Lennard et al., 1996). Resting whales were commonly grouped in maternal units. Individuals typically surfaced within a single body length of their neighbors (Barrett-Lennard et al., 1996).

Behavioral data were collected during months between April and October, during daylight hours, typically between 0700 and 2000. Waypoints were collected on the survey vessel at the beginning of each encounter, and at each instance in which there was a change of behavior. A 'group follow' protocol was used, where observers remain with a group for more than 30 minutes (Altmann, 1974). Data were collected using 'predominant group activity sampling,' where the activity of the majority of the group is noted (Mann 1999). The time, location, and behaviors were noted in field documentation and stored in GIS shapefiles.

Time spent in each behavior was calculated and compared between number of pods present, presence of rarely sighted pods, months, region, and genetic haplotype. Chi-squared tests were performed to examine overall behavioral budgets (Filatova et al., 2009; Saulitis et al., 2000; Morton 1990), and chi-squared tests were used to examine specific effects on each behavior. Twelve out of thirty-three pods were defined as 'rarely sighted' pods, which were seen in less than 5% of all encounters. For comparisons involving haplotype or 'rarely sighted' pods, encounters were excluded when only one pod was present. In order to minimize pseudoreplication, frequencies were obtained by sub-sampling the data only once per hour.

Biopsy samples were taken for >100 individual resident killer whales within the study area using the protocol established by Barrett-Lennard (2000) to determine haplotypic relationships. Analysis of the D-loop of the mitochondrial genome was used to determine

whether a sampled individual belonged to the SR, NR, or other haplotype (Barrett-Lennard, 2000).

2.4 Results

Behavioral observations were made over 1337 hours during 338 encounters in the months of May to October, between 2006 and 2015 (Table 2.1). Mean duration for behaviors ranged from 1.1 to 1.9 hours (Table 2.2). The mean number of pods present during encounters was 2.1 pods (SD=1.49), the median was 2 pods, and the mode was 1. The mean estimated number of animals present during encounters was 22.4 (SD=19.95), and the median was 16 individuals. The maximum number present during one encounter was 9 pods, with 116 whales photographed. As of 2015, the minimum population estimate as a result of this photo identification analysis was 708 resident killer whales (2015) from 33 pods.

The relative frequency of different behaviors varied significantly with the presence of 'rarely sighted pods' (sighted in less than 5% of total encounters) ($X^2 = 17.4, df = 3, P < 0.001$) and with number of pods present ($X^2 = 78.9, df = 9, P < 0.001$). Frequency of social behavior differed significantly ($X^2 = 17.3, df = 1, P < 0.001$) with the presence of at least one rarely sighted pod. Social behavior increased from 18.5% to 31.4% when rarely sighted pods were present. Frequency of social behavior also increased with the number of pods present ($X^2 = 72.8, df = 3, P < 0.001$). Social behavior was relatively rare during single pod encounters (4.7%), but increased with two pods present (16.1%), three pods present (21.2%), and four or more pods present (31.2%) (Figure 2.2). The number of genetic haplotypes present (one or two) did not contribute significantly to any difference in behavior ($X^2 = 0.46, df = 3, P =$

0.93). No difference was detected in the behavioral budget between encounters with only NR genetic haplotype whales vs. only SR genetic haplotype whales (Table 2. 4).

Frequency of foraging decreased significantly with the number of pods present ($X^2 = 12.7, df = 3, P = 0.005$), from 47.2% to 31.9% (Table 2.4, Figure 2.2). The frequency of resting behavior was significantly less (30.9% vs. 23.2%) when rarely sighted pods were present ($X^2 = 3.97, df = 1, P = 0.046$), than when no rarely sighted pods were present (Table 2.4, Figure 2.3). The frequency of behaviors did not differ significantly by region, haplotype, or number of haplotypes present.

The overall frequency of behaviors varied significantly by month ($X^2 = 34.4, df = 15, P < 0.001$). Specifically, seasonal differences were found in the frequency of foraging ($X^2 = 20.1, df = 5, P = 0.001$) and resting ($X^2 = 17.5, df = 5, P < 0.001$). Foraging was least frequent and resting was most frequent during July, August, and September. The frequency of social behavior was not significantly different among months ($X^2 = 6.9, df = 5, P = 0.227$). Rarely sighted pods and large multi-pod groups were found throughout the field season (Figure 2.4).

2.5 Discussion

Multi-pod aggregations of resident killer whales in southern Alaska appeared to occur for social purposes that likely included reproduction, and they occurred across the spring, summer, and fall field seasons. The increase in social behavior was pronounced when rarely sighted pods or multiple pods were present. Although not included as a category in the systematic behavioral observations, subjective observations indicate that there was often increased sexual activity during these multi-pod aggregations. Foraging was somewhat reduced, but remained the

predominant behavior. The presence of rarely sighted pods had the largest impact on the increase in social behavior.

The significant increase in social behavior with rarely sighted pods present was not surprising. Mating has been shown to occur primarily between pods that are acoustically unrelated (Barrett-Lennard, 2000), which would deter inbreeding. Increase of social behavior in Kamchatka has also been demonstrated when acoustically unrelated clans are found together (Filatova et al., 2009). Rarely sighted pods are likely to be acoustically and genetically differentiated, and to become a driver for reproductive activity. It is generally suspected and supported by satellite telemetry that the core use areas for rarely sighted pods are relatively distant (Matkin et al., 2013; Chapter 1) and that Prince William Sound and Kenai Fjords are on the edge of their range. In some cases, rarely sighted pods have been photographed with relative consistency in the neighboring regions of Kodiak or southeast Alaska (Matkin et al., 2013). Certain pods such as the AE pod in Prince William Sound (sighted in 24% of all encounters) have been documented through both satellite telemetry and photo-identification as having a linear home range spanning only 200km (Chapter 1). By contrast, the infrequently sighted AF and AG pods have been documented with photographs and telemetry as having a linear range of more than 1800 km. It is quite possible that Prince William Sound has enough rarely sighted visitors that a pod like the AE pod has no need to undertake such large movements to ensure genetic diversity within the pod. Mating and other social opportunities may drive the large observed ranges of the AF, AG, and AX pods.

Strong increase in social behavior and a concurrent decrease in foraging activity also support the importance of social interaction during these multi-pod encounters. Social activity and mating opportunities, and possibly the learning of mating skills, are suspected to be the

driver behind large aggregations of resident killer whales in Kamchatka (Filatova et al., 2009). Sexual behaviors are frequently noted during social behavior (Ford 1989). For transient killer whales in British Columbia, social behavior also increases when more than 7 individuals are present (Baird & Dill, 1996).

The reduction in foraging during multi-pod encounters supports the idea that cooperative feeding is not likely the cause of these large aggregations in southern Alaska. In Norway, killer whales aggregate to cooperatively forage on herring, but the group sizes are still relatively small (20-30 individuals) and the cooperative activity is obvious from the surface (Similä & Ugarte, 1993). Cooperative foraging has not been described in long-term studies of residents in Alaska or Canada (Ford et al., 1998, Saulitis et al., 2000), although prey sharing has been described, and may likely contribute to social bonds within matrilines and pods.

Foraging, though reduced during large aggregations, continued to be the predominant activity for any category, which implies that foraging is still important during these events. This is in contrast to findings during multi-pod events ('rare' foraging) in Kamchatka, but in agreement with encounters in the same location with 'several pods' (Filatova et al., 2009). The multi-pod encounters in that study, however, had a limited number of hours of observation.

Large aggregations in this study typically occurred in locations that are core use areas (Chapter 1). Resurrection Bay in Kenai Fjords and Hinchinbrook Entrance in Prince William Sound attract large multi-pod groups in early season, which is believed to result from high abundances of early season Chinook and chum salmon (Matkin et al., 2013). Montague Strait attracts large multi-pod groups in August through October, apparently due to inshore migration of coho salmon at that time (Matkin et al., 2013). Seasonality was not a significant factor toward changes in frequency of social behavior in this study, thus it is possible that social and

reproductive activity may be driven less by direct seasonality and more by the location and timing of efficient foraging opportunities that allows reduced foraging time and increased social activity typical of multi-pod aggregations. Season has been indicated as a driver for large groups in other studies, yet the explanation may simply be that seasonal runs of abundant salmon allow for these large groups to come together in productive locations at productive times (Hoelzel 1993). There is broad seasonality to large salmon returns in the northern Gulf of Alaska.

Some resident pods in this study population were as large as 40 whales (AJ pod) while others were as small as 6 whales (AD11 pod). Social activity may be more likely when whales from two small pods interact than when an equivalent number interact within a single larger pod. Thus, the number of pods present was considered a more meaningful analysis metric than the number of animals present.

No difference was detected in behavioral budgets between pods of the SR vs. NR genetic haplotypes. Additionally, no difference was noted in behavior budgets when large multi-pod events contained pods of different haplotypes. If social and mating behavior is more likely between unrelated pods (Barrett-Lennard, 2000), then one might expect there to be an increase in social behavior when pods of two different haplotypes are present. This was not the case in this study, so there may be sufficient genetic diversity among pods within the same haplotype that social behavior does not increase when pods of two different haplotypes are present. In Kamchatka, the presence of acoustically unrelated clans did contribute significantly to increased social behavior (Filatova et al., 2009).

Social behavior appears to be a driver for the large aggregations of resident killer whales that occur across seasons in Kenai Fjords and Prince William Sound. A significant increase in social activity occurs when rarely sighted pods travel into the region, and when there is an

increase in the number of pods present. Foraging behavior remains important during the large multi-pod encounters, and high abundance of salmon at the location of these events may be an important component in the aggregations. Details of the social interactions during these aggregations and a better understanding of their drivers deserve additional investigation.

2.6 Acknowledgements

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2.8 Figures:

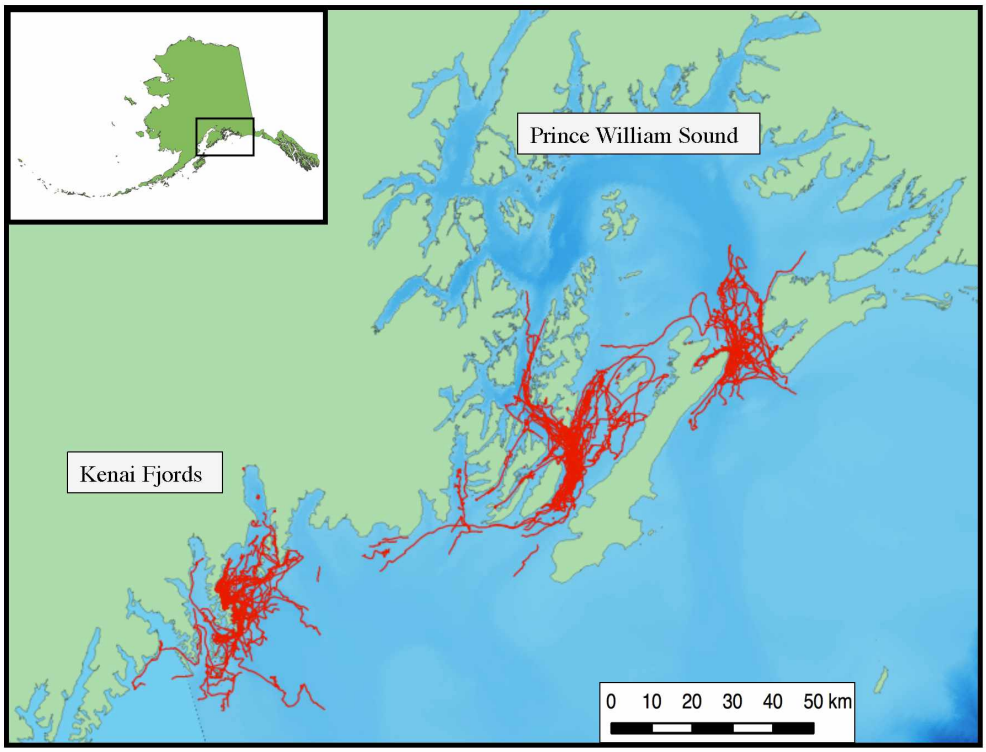

Figure 2.1. Prince William Sound and Kenai Fjords study area, with track lines of encounters with resident killer whales (*Orcinus orca*) from 2006 to 2015.

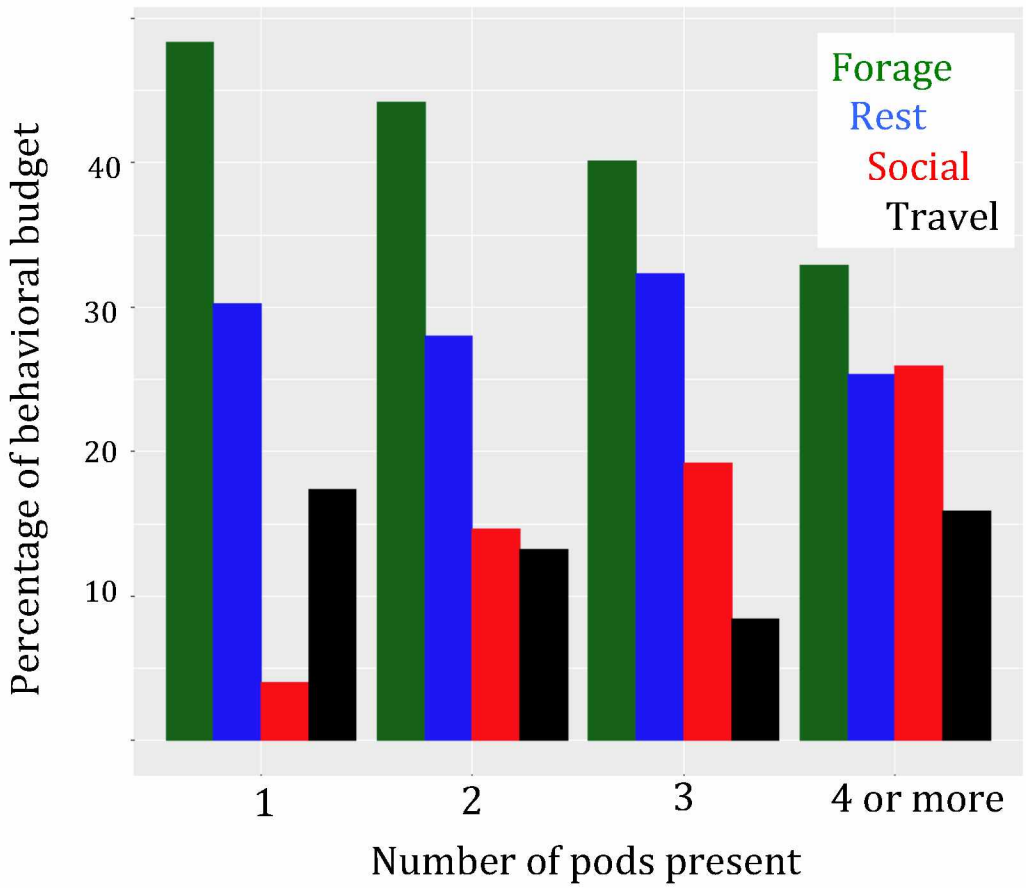

Figure 2.2. Percentage of time observed in each behavioral category by number of pods present.

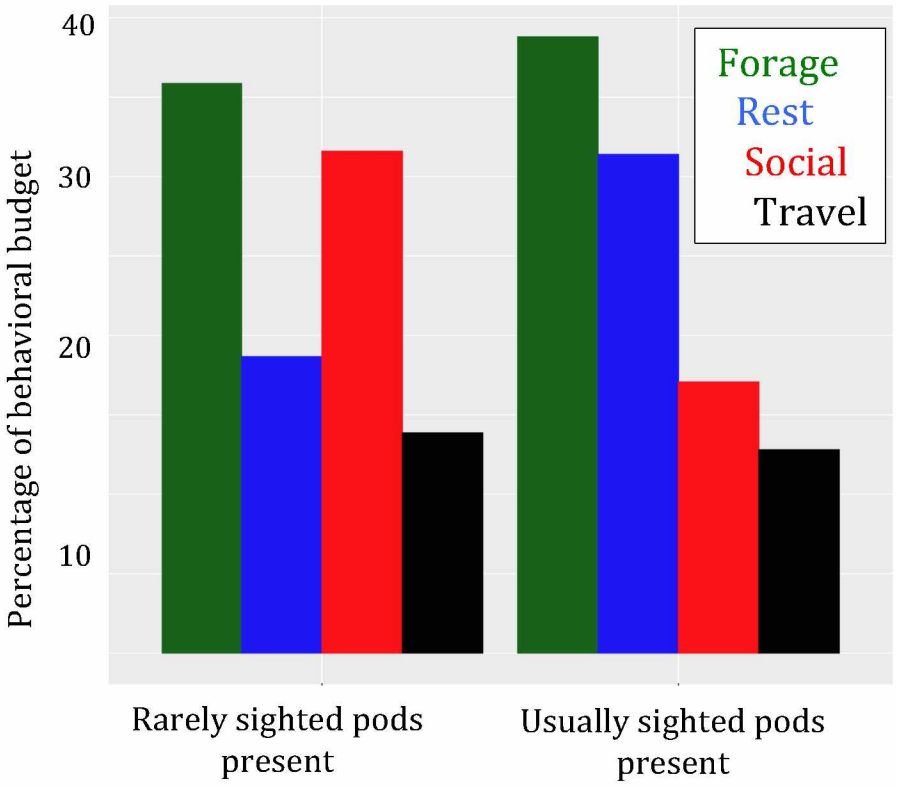

Figure 2.3. Percentage of time observed in each behavioral category with 'rarely sighted' pods present vs. usually sighted pods only.

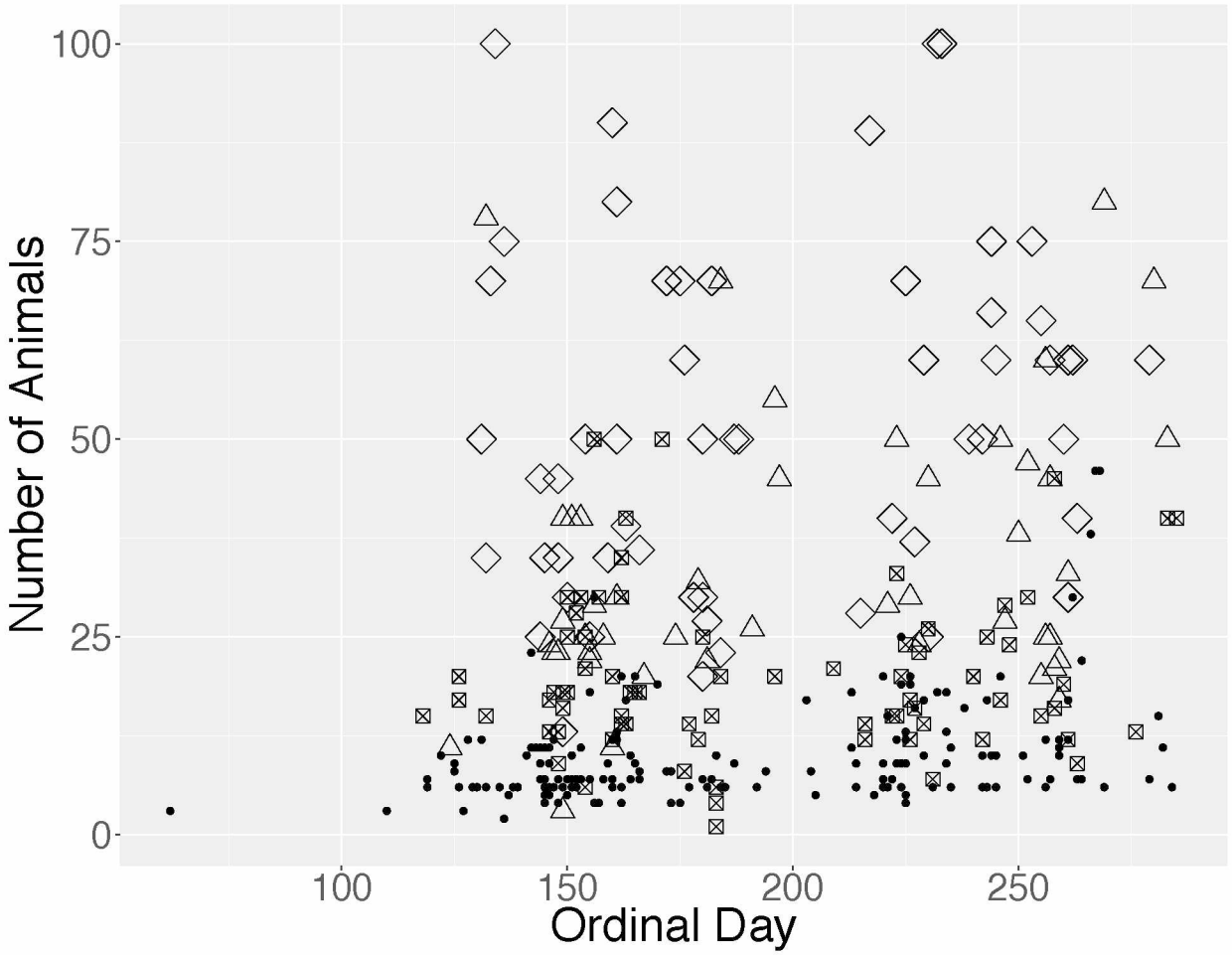

Figure 2.4. Number of pods and whales (estimated) present during encounters throughout the field season for all years, 2006 to 2015. Number of pods indicated by shape, black circle =1 pod, crossed square = 2 pods, triangle = 3 pods, diamond = 4 or more pods.

2.9 Tables

Table 2.1. Number of encounters and hours of behavioral observations with resident killer whales (*Orcinus orca*) by year.

Year	Encounters	Hours
2006	28	85.6
2007	28	141.0
2008	20	80.2
2009	39	190.2
2010	45	172.9
2011	44	178.2
2012	33	113.5
2013	20	68.0
2014	36	149.7
2015	45	158.1
Total	338	1337.4

Table 2.2. Mean and median duration of observed behaviors (hours) for resident killer whales (*Orcinus Orca*).

Behavior	Duration (mean, hours$\pm SD$)	(median, hours)
Forage	1.9 $\pm$1.5	1.5
Rest	1.7 $\pm$1.4	1.3
Social	1.7 $\pm$1.3	1.3
Travel	1.2 $\pm$1.0	0.9
ALL	1.7 $\pm$1.4	1.3

Table 2.3. Number of observations for each behavior by number or type of pods present.

Composition	Forage	Rest	Social	Travel	Total
One pod	202	129	20	77	428
Two pods	102	77	41	34	254
Three pods	79	67	45	21	212
Four or more pods	44	32	43	19	138
Regularly sighted pods only	246	199	119	79	643
Rarely sighted pods present	60	45	61	28	194

Table 2.4: Results of chi-squared and pairwise comparisons for behavioral categories.

Comparison	X^2	*df*	*p-value*
All behaviors by number of pods	54.7	9	< 0.001
Social behavior by number of pods	47.4	3	< 0.001
Forage behavior by number of Pods	12.2	3	0.007
All behavior by 'rarely sighted' pods present	14.6	3	0.002
Social behavior 'rarely sighted' pods present	10.6	1	0.001
Rest behavior by 'rarely sighted' pods present	6.6	1	0.01
All behaviors by region	6.3	3	0.10
All behaviors by season	3.8	6	0.70
All behaviors by number of haplotypes, 1 or 2	0.46	3	0.93
All behaviors, NR vs. SR haplotype	1.8	3	0.62

General Conclusions

Differences between core use areas occurred seasonally for resident killer whales in the northern Gulf of Alaska, and were specific to individual pods. The observed differences in core use areas were likely related to the specific timing of returns of Chinook, chum and coho salmon to their natal spawning streams, and the congregation of Chinook salmon while foraging in nearshore waters. Salmon perform highly predictable seasonal returns to their natal streams, and Chinook, coho, and chum salmon have been shown to comprise a major portion of the summer diet for resident killer whales in south central Alaska (Matkin et al., 2013; Saulitis et al., 2000). The arrival of resident killer whales and salmon has been shown to occur concurrently in British Columbia (Hanson et al., 2010), and Chinook and coho salmon have been shown to dominate the summer diet of resident killer whales in that area (Ford & Ellis, 2006; Ford et al., 2016). Survival rates for resident killer whales in British Columbia have been linked with abundance of Chinook salmon (Ford et al., 2010). In Alaska, prey samples have been collected at three of the high-use areas noted in this study, and were dominated by scales from Chinook, coho, and chum salmon (Matkin et al,. 2013; Saulitis et al., 2000). Seasonal dietary shifts from Chinook to coho have been documented in both Alaska and the Pacific Northwest (Ford et al., 2016; Matkin et al., 2013).

The Alaska Department of Fish and Game reports peak chum return timing to occur in late June in Prince William Sound (ADFG, 2002), which could be partially responsible for the high use of Hinchinbrook Entrance in early summer. Chum salmon scales from predation by resident killer whales have been collected in Hinchinbrook entrance in June (Matkin et al., 2013). Hinchinbrook Entrance is one of the two main entrances to Prince William Sound, and is the main influx of water into the sound (Halverson et al., 2013).

The high use in Montague Strait in late summer and fall coincides with large congregations of adult Pacific herring (*Clupea pallasi*) and humpback whales (*Megaptera novaeangliae*) that prey on them (Moran et al., 2015). Although herring are important in the diet of killer whales in Norway and Iceland, the technique for hunting them is evident from the surface (Samarra & Foote, 2015; Similä et al., 1996). Herring predation is very rare for killer whales in the North Pacific based on extensive observations from surface kill remains and scat analysis (Ford & Ellis, 2006; Ford et al., 2016; Saulitis et al., 2000). It is likely that this aggregation of herring attracts feeding Chinook and coho salmon, the latter two being key prey items for resident killer whales in southern Alaska.

Pod-specific habitat preferences described in the present study are likely the result of cultural transmission of learning through generations, as individuals swim with their mother or close relatives throughout their lives (Bigg et al., 1990). Cultural transmission has been documented amongst killer whale acoustic repertoires, foraging strategies, and habitat preferences (Guinet & Bouvier, 1995; Hauser et al., 2007; Similä & Ugarte, 1993; Yurk et al., 2002). Similar patterns in pod-specific core use were noted in the San Juan Islands for SRKW (Hauser et al., 2007). Another possible cause of pod-specific use patterns could be explained by territorial exclusion, but acts of aggression between unrelated pods were not observed. To the contrary, killer whale pods are often attracted to unrelated pods for social and reproductive reasons. Furthermore, closely related pods in chapter one of this thesis demonstrated similar patterns of habitat use. AB, AI, and AJ pods share the NR haplotype, and are the only pods shown to use offshore waters west of Kayak Island and Hinchinbrook Entrance. AD16 and AK pods share the SR haplotype, and are the only pods to use upper fjords and to focus on nearshore habitat. Pod-specific behavior may be a mechanism to avoid resource competition.

The difference in linear range between the AE pod (roughly 200 linear km) which has the SR haplotype, and the AF and AG pods (1300 linear km) which have the NR haplotype, is striking. While this difference could be attributed to diet differences, it is more likely that these differences in linear range stem from social and reproductive needs (Matkin et al., 1997).

Bathymetry appears to be important in some core use areas, and should be explored further. Our results show that the deeper waters (200-300m) of Montague Strait are important during summer and fall. Bathymetric features have been found to be preferential habitat for other delphinids (Dahood, 2009; Ingram & Rogan, 2002). Depth sensors were present on a limited number of tags in this study, and suggest that resident killer whales in this area regularly dive to or near the seafloor in 200-300m (Matkin et al., 2013). Chum salmon in Japan have been observed to dive to the bottom in response to presence of Dall's porpoise (*Phocoenoides dalli*) (Yano et al., 1984), and Chinook salmon have been documented diving 300-400m after release (Candy & Quinn, 1999). Furthermore, DTAGs deployed on NRKW in British Columbia documented the capture of Chinook, chum, and coho salmon as deep as 264, 164, and 165m respectively (Wright, 2014). If salmon aggregate in these deep basins near the entrances to avoid predation, or to feed on congregating forage fish such as herring, the use of deeper waters within Montague Strait and near Kayak Island could be explained. Interestingly, many other deep glacial trenches in the continental shelf do not appear to be important for these Gulf of Alaska resident killer whales during the summer and fall.

Alternatively, the deep waters of Montague Strait, Hinchinbrook Entrance, and Kayak Island could provide important foraging opportunities on benthic species, including Pacific halibut (*Hippoglossus stenolepis*), lingcod (*Ophiodon elongatus*), and sablefish (*Anaplopoma fimbria*). It would be unlikely to collect tissue samples from predation events on these species at

the surface if they were consumed in deeper waters. However, in spite of the availability of these potential prey species in other deep waters at the edge of the continental shelf and in the deep glacial trenches that cut across the shelf, these other deep-water locations were not used much by tagged individuals in this study. Additionally, recent studies of killer whale fecal samples from the SRKW population in the San Juan Islands demonstrate similar findings to the surface collections of fish scale and tissue after predation events, which is that salmonid prey dominate the diet in summer months (Ford et al., 2016). The seasonality of use by killer whales in Montague Strait, Hinchinbrook Entrance, and Kayak Island also supports surface observations of salmon predation (Matkin et al., 2013; Saulitis et al., 2000).

One of the important revelations of this project, and one of the main advantages of satellite telemetry over other methods of habitat assessment, was the discovery of previously unknown core use areas. The region just west of Kayak Island appears to be important habitat, particularly in June, July, and August (Figure 1.2). Additionally, the areas SE of Marmot Island and NE of Shuyak Island appear to be important for at least the AD5 and AY pods (Figure 1.5). Due to the remote location and difficult weather conditions, these areas would not likely be revealed by boat surveys, which can be biased by survey effort (Baird et al., 2010). Interestingly, most of the use near Kayak Island was from AB, AI, and AJ pods, and nearly every tagged member of AB, AI, and AJ pods visited this area. In the future, passive acoustics may help detail the importance of these areas.

The variability described in this study serves as a caution for estimation of home range. Culturally influenced, pod-specific behavior appeared to have great impact on home range size estimates. Home range sizes for individuals from AB, AE, AI, and AJ pods were all limited to 20,000 sq. km. or less, while individuals from AF, AG, and AX pods had home ranges of nearly

30,000 sq. km. These differences did not appear to be a result of tag transmission duration, and the home ranges based on these telemetry data are very similar to the geographic extent of photographic documentation (C. O. Matkin, unpubl. data). AB, AE, AI, and AJ pods have never been photographed beyond the relatively small range represented by the tag data, and the home ranges of AF and AG pods are also very similar to the photographic documentation, which extends from Kodiak to southeastern Alaska (Matkin et al., 1997). Without consideration of these cultural and behavioral differences, any study that has a limited number of tags may illustrate a subset of the population that is not representative of the whole.

The median short-term movement estimates of 4.43 km/hr (106 km/day) calculated in chapter one are similar to published movement rates for NRKW of 1.6 m/s (138 km/day) calculated by theodolite (Williams & Noren, 2009). However, these estimates are likely a conservative estimate, as some non-linear movements are not always documented if there are gaps in the tag data.

The strong temporal patterns and pod-specific core use described in the present study should be considered in conservation management strategies. As an example, vessel traffic in the oil tanker lanes through Hinchinbrook Entrance may have a much larger impact on resident killer whales in June and July than in September and October, and impact by winter vessel traffic is largely unknown. Additionally, the AB pod, which lost 25% of it members after swimming through the Exxon Valdez Oil Spill in 1989 (Matkin et al., 2008), appears to depend heavily on Hinchinbrook Entrance, Montague Strait, and the waters west of Kayak Island. Restoration plans for this pod should consider the protection of these areas. Future research should investigate the relationship between seasonal differences in core use and salmon migration routes, and also investigate wintertime use.

Large aggregations of resident killer whales were documented in some of these core use areas, and appeared to occur for social purposes that likely included reproduction. They occurred across the spring, summer, and fall field seasons. The increase in social behavior was most pronounced when rarely sighted pods (photographed in <5% of encounters) were present. Subjective observations indicate that sexual activity was increased during these multi-pod aggregations, although it was not included as a category in our systematic behavioral observations. Foraging was somewhat reduced during these social aggregations, but remained the predominant behavior. The presence of rarely sighted pods had the largest impact on the increase in social behavior.

The significant increase in social behavior when rarely sighted pods were present was not surprising. Mating has been shown to occur primarily between pods that are acoustically unrelated (Barrett-Lennard, 2000), promoting genetic diversity. Rarely sighted pods are likely to be acoustically and genetically distinct, and to become a driver for reproductive activity (Barrett-Lennard, 2000). It is generally suspected, and is supported by satellite telemetry, that the core use areas for 'rarely sighted' pods are relatively distant (Matkin e al., 2013; Chapter 1) and that Prince William Sound and Kenai Fjords are on the edge of their range. In some cases, rarely sighted pods have been photographed with relative consistency in the neighboring regions of Kodiak or southeast Alaska (Matkin et al., 2013). Certain pods such as the AE pod in Prince William Sound (sighted in 24% of all encounters) have been documented through both satellite telemetry and photo-identification as having a linear home range spanning only 200 km (Chapter 1). By contrast, the infrequently sighted AF and AG pods have been documented with photographs and telemetry as having a linear range of more than 1800 km. The very large range

of some resident killer whale pods may be driven primarily by social opportunities that include mating.

Strong increases in social behavior and a concurrent decrease in foraging activity also supports the importance of socialization during these multi-pod encounters. Social activity and mating opportunities, and possibly the learning of mating skills, are suspected to be the driver behind large aggregations of resident killer whales in Kamchatka (Filatova et al., 2009). Sexual behaviors are noted during social behavior (Ford 1989). For transient killer whales in British Columbia, social behavior was shown to increase when more than 7 individuals are present (Baird & Dill, 1996). While seasonality has been suspected as a covariate for resident social and mating activity, our findings do not show significant differences in social behavior between the spring, summer, and fall periods.

Foraging, though reduced during large aggregations, continued to be the predominant activity for any category, which implies that foraging is still important during these events. This is in contrast to findings during multi-pod events ('rare' foraging) in Kamchatka, but in agreement with their encounters with 'several pods' (Filatova et al., 2009). The multi-pod encounters in that study, however, had a limited number of hours of observation.

Large aggregations in this study occurred in locations that are typically core use areas (Chapter 1). Resurrection Bay in Kenai Fjords and Hinchinbrook Entrance in Prince William Sound attract large groups in early season, which is believed to result from abundance of early season Chinook and chum salmon (Matkin et al., 2013). Montague Strait attracts large groups in August through October, apparently due to inshore migration of coho salmon at that time (Matkin et al., 2013). Social and reproductive activity may be driven less by seasonality and more by the location and timing of efficient foraging that allows reduced foraging time and

increased social activity typical of multi-pod aggregations. Season has been indicated as a driver for large groups in other studies, yet it could be simply that seasonal runs of abundant salmon allow for these large groups to come together in productive locations at productive times (Hoelzel 1993).

The reduction in foraging supports the idea that cooperative feeding is not likely the cause of the large aggregations. In Norway, killer whales aggregate to cooperatively forage on herring, but the group sizes during these events are smaller (20-30 individuals) than the large multi-pod aggregations discussed here, and the activity is obvious from the surface (Similä & Ugarte, 1993). Cooperative foraging has not been described in long-term studies of residents in Alaska or Canada (Ford et al., 1998, Saulitis et al., 2000), although prey sharing has been described, and may likely contribute to social bonds within matrilines and pods.

Some resident pods in this study population were as large as 40 whales (AJ pod) while others are as small as 6 whales (AD11 pod). Social activity may be more likely when whales from two small pods interact than an equivalent number of whales from one larger pod. For analysis, number of pods present was considered a more meaningful metric than the total number of animals present.

It is rather interesting that there was no difference detected in behavioral budgets between pods of one genetic haplotype or the other. Additionally, it was interesting to note that there was no significant difference when a multi-pod event contained pods of both NR and SR haplotypes. If social and mating behavior is more likely between unrelated pods (Barrett-Lennard, 2000), then one might expect there to be a change in social behavior when pods of both haplotypes were present. This was not the case, so there may be sufficient diversity within each of the two haplotypes (NR and SR) that social behavior is not influenced by haplotype alone.

From this study there are several main conclusions. First, core use areas in this population are specific to pod, possibly due to cultural transmission within matrilineal groups. The second is that there are distinct seasonal shifts in core use areas. These seasonal shifts are most likely in response to the migratory return and feeding congregations of various species of salmon. Social behavior appears to be important for resident killer whales, and a significant increase in social behavior occurs relative to the presence of rarely sighted pods, and to the number of pods present. Surprisingly, season was not a strong indicator of percentage of time engaged in social behavior, but timing of social behavior may be generally related to abundant salmon returns, especially given that foraging behavior remained important during these social events. Continued diet studies are warranted to investigate relationships between spatial shifts and the subsequent prey, and the relationship between large social aggregations and timing of abundant prey. Further investigations into synchronous estrus, mating events, and birthing events may inform timing and purpose of social aggregations. Lastly, future studies should consider that large ranges could be driven more by mating opportunities and social activity than by foraging opportunities.

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